single ovule. Professor Hitchock (personal letter to William H. Rickard, 22 November 1960) pointed out the intermediacy of *L. rickardii* between *L. californicum* and "such species as *L. macrodon* and *L. puberulum*." It might be added that both *L. rickardii* and *L. shockleyi* stand in this position with *L. rickardii* closer to *L. californicum* and *L. shockleyi* more similar to *L. macrodon* Gray, *L. puberulum* Gray, and *L. cooperi* Gray.

It is extremely likely that *L. rickardii* is somewhat more widely distributed than at present known. In the rather copious material at hand there is no evidence that heavy doses of irradiation at the Test Site are in any way responsible for the characters of *L. rickardii*. The longevity of these plants insures their being older than the Test Site, and their essential uniformity with those of the southerly and southeasterly range of the species makes it highly unlikely that the characters here noted might have arisen as a result of somatic mutation.

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SOME RECENT OBSERVATIONS ON PONDEROSA, JEFFREY AND WASHOE PINES IN NORTHEASTERN CALIFORNIA

John R. Haller

In an earlier paper (1959), I suggested that *Pinus jeffreyi* Grev. and Balf. is less susceptible to cold than is *P. ponderosa* Dougl. ex Lawson, and that for this reason *P. jeffreyi* replaces *P. ponderosa* at high altitudes in the mountains of California. Dr. Willis W. Wagener reported recently (1960), however, that established trees of *P. ponderosa* survived at least as well and occasionally better than *P. jeffreyi* following periods of severe cold in northeastern California. The purpose of the present paper is to present additional information on the pines of northeastern California which I believe will show that there is no discrepancy between Wagener's observations and my own, and that, in fact, they even reinforce one another.

In our respective papers, Dr. Wagener and I were discussing examples from different areas—his from northeastern California, mine mostly from cismontane California, that portion of the state lying to the west of the Sierra-Cascade crest. I deliberately omitted a discussion of the northeastern Californian pines because the great bulk of the Ponderosa Pine in California occurs in the cismontane portion of the state, and because northeastern California is climatologically and floristically more closely related to the Great Basin region than to the rest of California. In addition, the ecological, genetic, and taxonomic relationships of the pines in northeastern California appear to be far more complex than in the remainder of the state. I am currently preparing a paper which will attempt to describe their relationships with each other and with the pines farther to the east.

There is considerable evidence available which supports the idea that *Pinus ponderosa* from cismontane California is more susceptible to low temperatures than either *P. jeffreyi* or *P. ponderosa* from more interior localities. The precise altitudinal zonation on the western slope of the Sierra Nevada, with *P. ponderosa* occupying the lower elevations and *P. jeffreyi* occupying the higher, is very suggestive of a difference in cold tolerance (Table 1). As I have indicated previously (1959), in the narrow zone where these species overlap, *P. jeffreyi* nearly always occupies the colder sites, such as canyon bottoms and the margins of low-lying meadows. Pearson (1931) reported that first-year seedlings of *P. ponderosa* from the Sierra National Forest (on the western slope of the Sierra Nevada) planted near Flagstaff, Arizona, were killed by a November freeze,[1] whereas seedlings from several other western states planted at the same locality were not injured. Weidman (1939) reported that young trees of *P. ponderosa* from the vicinity of Weed, California (west of the Cascade crest), planted near Sandpoint in northern Idaho were killed at the age of 12 years when the temperature fell rapidly from 45°F to —12°F. Trees of approximately the same age from 19 localities in Oregon, Washington, Idaho, Montana, South Dakota, Colorado, Utah, New Mexico and Arizona, planted in the same site as the Californian trees, survived the cold. Temperatures lower than —12°F occasionally occur within the range of *P. jeffreyi* in the western Sierra Nevada and within the range of both *P. ponderosa* and *P. jeffreyi* in transmontane northeastern California, but virtually never within the cismontane range of *P. ponderosa* (Table 1). The temperatures shown in Table 1 are the lowest that occurred in 1949, which was a year of record-breaking cold for many of the stations. This is the same year that Wagener observed fairly extensive damage to both *P. ponderosa* and *P. jeffreyi* in California. Table 1 shows that *P. ponderosa* occurs in the warmer cismontane localities and *P. jeffreyi* in the colder, but in transmontane California the two species grow in equally cold localities which are frequently colder than the coldest cismontane *P. jeffreyi* localities.

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[1] Neither the temperature nor the year of its occurrence were given by Pearson. However, the coldest November temperature on record for Flagstaff for the years 1906–1930 is —4°F. This is probably not sufficiently cold to kill mature *P. ponderosa* from cismontane California (see Table 1), but was cold enough to be fatal to the more susceptible seedlings.

TABLE 1. MINIMUM TEMPERATURES IN 1949 IN CALIFORNIA.
Based on official records of the United States Weather Bureau*

A. Cismontane Localities

LOCALITY	COUNTY	ELEV.	TEMP.
Ponderosa Zone			
Placerville	Eldorado	1900 ft.	14°F
Sierra City	Sierra	4200	5°
Calaveras Grove	Calaveras	4800	5°
Yosemite Valley	Mariposa	4000	2°
Mt. Shasta (town)	Siskiyou	3500	1°
South Entrance, Yosemite N. P.	Mariposa	5100	—3°
Ponderosa-Jeffrey Zone			
Giant Forest	Tulare	6400	—4°
Grant Grove	Tulare	6700	—6°
Lake Spaulding	Nevada	5000	—8°
Jeffrey Zone			
Manzanita Lake	Shasta	5800	—3°
Huntington Lake	Fresno	7000	—10°
Twin Lakes	Alpine	7900	—24°
Soda Springs	Nevada	6700	—27°

B. Transmontane Localities

LOCALITY	COUNTY	ELEV.	TEMP.
Ponderosa Zone			
Cedarville	Modoc	4700 ft.	—20°F
Mount Hebron	Siskiyou	4200	—22°
Alturas	Modoc	4300	—31°
Ponderosa-Jeffrey Zone			
Truckee	Nevada	6000	—19°
Sierraville	Sierra	5000	—25°
Boca	Nevada	5500	—41°
Jeffrey Zone			
Woodfords	Alpine	5600	—10°
Bridgeport	Mono	6400	—31°

* In some of the localities listed above, the species concerned does not occur in the immediate vicinity of the weather station. However, discrepancies between weather station temperatures and those in the adjacent pine localities have been kept to a minimum by selecting stations in situations that are ecologically similar to the pine localities and never more than a few miles removed from them. Stations have also been selected to show the maximum temperature variation within each zone.

The evidence given above indicates that *Pinus ponderosa* from northeastern California is different physiologically from that on the cismontane slopes, since it survives temperatures lower than those that have killed cismontane *P. ponderosa* in experiments. This physiological difference is reflected in the relative distribution of *P. ponderosa* and *P. jeffreyi* in northeastern California, where these two species occur together over much more extensive areas than on the western slopes of the mountains. Furthermore, there is no tendency for *P. jeffreyi* to occupy the colder sites within these extensive mixed stands, as occurs on the cismontane slopes.

In addition to the physiological—distributional differences between cis- and transmontane *Pinus ponderosa,* there are morphological differences. To begin with, the *P. ponderosa* from northeastern California is far more variable than that in the western Sierra Nevada, ranging from essentially identical to that farther west to something strikingly different. Because of this high variability, it is difficult to generalize about particular character differences. However, one character, needle thickness, shows relatively consistent differences between the west and east sides of the Sierra-Cascade crest. In all of the cismontane localities where I have measured needle thickness in mixed stands of *P. ponderosa* and *P. jeffreyi,* the mean thickness is greater in *P. jeffreyi.* In the typical examples given in Table 2A, the needles of *P. jeffreyi* average 0.19 mm. thicker than those of *P. ponderosa,* and the difference between the two species is highly significant at each of the three localities shown. Just the reverse is true on the east side of the Sierra-Cascade crest, where the needles of *P. ponderosa* average 0.12 mm. thicker than those of *P. jeffreyi* (Table 2B). However, east of the crest the differences between the species range from essentially nil at Sierraville to very pronounced at Hobart Mills. It is noteworthy that at Sierraville, where the needles of *P. ponderosa* are thinnest, the population is not unusually variable and is in most respects very similar to cismontane *P. ponderosa.* On the other hand, the *P. ponderosa* near Hobart Mills, which has much thicker needles than *P. jeffreyi,* is tremendously variable and for the most part very different from cismontane *P. ponderosa* (Haller, 1957). This thick-needled Hobart Mills population is located just three miles from Boca, which frequently has the lowest winter temperatures of any station in California (Table 1), suggesting that thick needles may be adaptively advantageous in cold climates.

There are at least three possible causes for the physiological and morphological differences between the cis- and transmontane *Pinus ponderosa* in northern California: environmental modification, differential selection from a heterozygous gene pool, and introgressive hybridization. A certain amount of environmental modification no doubt occurs in all populations of *P. ponderosa,* as the experiments of Weidman, the Institute of Forest Genetics, and my own observations (1957 and in press) have shown. However, these same experiments and observations show that the greater proportion of all physiological and morphological traits is genetically determined and cannot be ascribed solely to modification. Selection from a heterozygous gene pool has probably been the principal mechanism that has enabled *P. ponderosa* to occupy so many diverse habitats in western North America and to differentiate into a number of geographical races or subspecies. The geographical pattern of variation shown by these races is, however, a subtle one, and I have found that the

TABLE 2. MEAN NEEDLE THICKNESS IN PONDEROSA, JEFFREY AND WASHOE PINE POPULATIONS

Locality	County	Elevation (feet)	Sample Size	Mean Needle Width: Ponderosa	Mean Needle Width: Jeffrey	Significance of Difference
A. Cismontane Localities						
Silver Fork, American River	Eldorado	6400	10	1.32 mm.	1.54 mm.	.004
Ebbetts Pass Highway	Calaveras	6300	24	1.60	1.75	.005
Shasta Valley	Siskiyou	4500	25	1.65	1.83	<.001
Mean of cismontane Ponderosa and Jeffrey populations:				1.52	1.71	
B. Transmontane Localities						
Sierraville	Sierra	5000	25	1.78	1.78	......
Dixie Mtn. Game Refuge	Plumas	5700	10	2.01	1.88	.075
Hobart Mills	Nevada	5800	50	2.10	1.87	<.00003
Mean of transmontane Ponderosa and Jeffrey populations:				1.96	1.84	
				Washoe	Jeffrey	
Mt. Rose, Nev.	Washoe	7200	25	2.05 mm.	1.88	.0006
Warner Mtns.	Modoc	7500	14	2.13	2.02*	.10
Mean of transmontane Washoe and Jeffrey populations:				2.09	1.95	

* The Warner Mountain Jeffrey Pine population is not sympatric with the Washoe Pine population, but is located a few miles away.

overall variability of the populations is usually about the same from one locality to the next. As already stated, many of the *P. ponderosa* populations in northeastern California differ strikingly from nearby populations and also display great variability. Such a pattern would be expected if hybridization were taking place.

The probable introgressant of *Pinus ponderosa* in northeastern California is *P. washoensis* Mason and Stockwell. One of the more outstanding characters of *P. washoensis* is its thick needles, which also characterize the variable *P. ponderosa* populations at Hobart Mills and Dixie Mountain Game Refuge (Table 2B). In addition there are other characters of *P. washoensis*, such as compact cones and short needles, which are prevalent in these variable *P. ponderosa* populations. I am still in the process of analyzing data from *P. ponderosa, P. washoensis,* and *P. jeffreyi* in northeastern California, but I am reasonably certain that the hybridization suggested here will be confirmed by further investigation.

The only published record of *Pinus washoensis* is from the type locality, on the watershed of Galena Creek, Mount Rose, Washoe County, Nevada (Mason and Stockwell, 1945). This locality is about 14 miles east of the Hobart Mills *P. ponderosa* population. A much more extensive stand of *P. washoensis* occurs in the Warner Mountains, Modoc County, California. The best stands, which include many trees that are four feet in diameter, are located in the southern part of the range, in the general vicinity of the Patterson Ranger Station. Specimens from this area have been deposited in the herbarium of the University of California at Santa Barbara. Both the Mount Rose and Warner Mountain stands of *P. washoensis* occur above the 7000 foot elevation, apparently too high for *P. ponderosa.* The Mount Rose stand occurs sympatrically with *P. jeffreyi,* whereas the Warner Mountain stand occurs almost entirely above a narrow zone of *P. jeffreyi.* Additional stands of typical *P. washoensis* might well occur on other sufficiently high peaks in northeastern California. *Pinus washoensis* also occurs sporadically at lower elevations, for example in the variable "*P. ponderosa*" population near Hobart Mills. Very few individuals at this locality are "good" *P. washoensis,* but many of the trees in this apparent hybrid swarm are more similar to *P. washoensis* than they are to typical *P. ponderosa* (Haller, 1957).

The factors which limit the distribution of individuals of taxa such as *Pinus ponderosa, P. jeffreyi,* and *P. washoensis* are extremely difficult to circumscribe exactly. However, some idea of the relative cold susceptibilities of members of these taxa might be obtained from a series of experiments. For example, seeds of *P. ponderosa* and *P. jeffreyi* from the same site in the western Sierra Nevada and from northeastern California could be grown under uniform conditions, and the seedlings subjected to increasing intensities of cold. If a sufficient number of experiments were made, it would be apparent whether *P. ponderosa* is ever more susceptible to cold than *P. jeffreyi,* or if either or both species vary from one locality to another in their relative susceptibility. The results of any such experiments would have to be interpreted with caution, however. For example, *P. ponderosa* and *P. jeffreyi* from the same site in the western Sierra Nevada (near the upper altitudinal limit of the former and the lower limit of the latter) might be found to have an identical tolerance for cold. The upward migration of *P. ponderosa* could nonetheless be checked at this point by cold, because the species has exhausted its genetic potential for cold tolerance. *Pinus jeffreyi,* on the other hand, could have a much greater potential cold tolerance, which might be expressed only at higher altitudes, where it would be favored by natural selection.

The possibility also exists that the upward migration of *Pinus ponderosa* is not checked by low winter temperatures, but by insufficiently high temperatures during the growing season. Pearson (1931) stated that low summer temperatures are the principal deterrent to the success of *P. ponderosa* when it is planted at elevations above its normal range in the San Francisco Mountains of Arizona. In this region, *P. ponderosa* is limited to the valleys and lower slopes of the mountains where summer maximum temperatures are higher but winter minima are lower than in the Douglas Fir zone immediately above.

Evidence has been submitted in this paper that *Pinus ponderosa* from cismontane California is more susceptible to cold than is *P. jeffreyi,* that *P. ponderosa* from northeastern California is at least as tolerant of cold as is *P. jeffreyi* and that the spread of *P. ponderosa* to higher elevations is checked in Arizona by low summer temperatures rather than by extremes of cold in winter. Most of this evidence is indirect, and a more precise determination as to the factor or factors which limit *P. ponderosa* in its many different habitats will have to await the outcome of future experiments. For the present, it appears reasonable to postulate that low temperatures, whether in the form of low winter minima or low summer maxima, play an important role in limiting the distribution of *P. ponderosa.*

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INFLUENCE OF TEMPERATURE AND OTHER FACTORS ON CEANOTHUS MEGACARPUS SEED GERMINATION

Elmer Burton Hadley[1]

One of the striking characteristics of chaparral is the absence of any kind of seedlings beneath mature, undisturbed stands. After such disturbances as bulldozing or fire, however, an abundance of seedlings appears, suggesting that scarification or heat make the germination possible (Cooper 1922, Went *et al.* 1952, Horton & Kraebel 1955, Quick 1959).

The density and dryness of this chaparral brush cover in California, the accumulation of large quantities of dry litter beneath the brush, and the Mediterranean type climate, all combine to create an extreme fire

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